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Predation risk and the opportunity for female mate choice in a coral reef fish

Abstract The influence of predation risk on the opportunity for female mate choice was investigated in the tailspot wrasse *Halichoeres melanurus* at two sites on a coral reef in Okinawa, Japan. Females mated repeatedly with the nearest males, but they also changed mates frequently at both sites. Mate changes were seen not only in the context of spatiosocial changes (mate disappearance or shifts in male territories) but were also probably the result of actual mate choice by females. Females at one site (site A) changed mates more often and conducted longer spawning trips from their home ranges to male territories than at the other site (site B). Fish at site A were faced with a higher frequency of predators than that of site B. However, fish of site A suffered fewer attacks from predators because they had more shelter, suggesting lower predation risk in that site. These results suggest that females under higher predation risk had less opportunity to choose preferable mates and that they had to mate with the same, nearest males in most cases.

Key words Female mate choice · Predation risk · Mating system · Female mate-change behavior · *Halichoeres melanurus*

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Introduction

Female mate choice is a main component of sexual selection (Darwin 1871) and has been investigated, both theoretically and empirically, from various aspects (Bateson 1983; Andersson 1994). Females usually choose the "best" mates for their direct or indirect benefits (Fisher 1930; Zahavi 1975; Hamilton and Zuk 1982; Kirkpatrick and Ryan 1991; Pomiankowski et al. 1991). However, female choosiness is often affected by environmental factors. For example, when costs of mate choice are large or male availability is low, females become less choosy and often attempt to mate with males indiscriminately (e.g., sticklebacks [*Gasterosteus aculeatus*], Bakker and Milinski 1991; guppies [*Poecilia reticulata*], Houde 1997).

Predation is a major component of the environmental factors that may affect the reproductive behavior of animals (Magnhagen 1991; Sih 1994). Under high predation risk, females should reduce their choosiness to decrease their vulnerability to predators during mate searching and comparison. Only a few studies, however, have documented the effect of predation risk on female choice, and most were conducted in the laboratory (Forsgren 1992; Hedrick and Dill 1993; Godin and Briggs 1996; Gong and Gibson 1996). Field studies may show only indirect evidence, such as a change in male traits or female mate preferences between habitats with different predation risks (Endler 1983; Endler and Houde 1995). The purpose of the present study is to examine how predation risk affects female mate choice in the tailspot wrasse, *Halichoeres melanurus*, under natural conditions.

The tailspot wrasse is a protogynous fish (Kuwamura et al. 2000), distributed in the Western Pacific, and shows remarkable sexual dichromatism (Masuda et al. 1984; Randall et al. 1990). Larger males assume a conspicuous coloration (terminal phase, TP) on their body and fins, while females are small with drab coloration. TP males establish mating territories in which pair-spawning with females occurs at dusk (Colin and Bell 1991; Kuwamura et al. 2000). Colin and Bell (1991) reported that the tailspot

wrasse was haremic, i.e., a single male monopolizes several females and females mate with the same male repeatedly. However, our preliminary observation showed that individual females may change their mates daily. Moreover, female tailspot wrasses show a clear mate preference for larger males with brighter coloration (Kuwamura et al. 2000). From the point of view of female mate choice, females should change subsequent mates if they find a more preferable individual than their previous mate. Thus, female mate choice in the tailspot wrasse may be the cause of their mate-change behavior. In this study, we compare female mate-change behavior between two adjacent study sites with different topographies and putative predation risk. We then discuss the effects of predation risk, with regard to topographical difference, on the opportunity for female mate choice.

Materials and methods

Field observations were conducted using SCUBA or snorkel on the fringing reef of Sesoko Island, Okinawa. We chose two sites, A and B, in close proximity (about 15 m apart; Fig. 1). Both sites included reef edges, as male tailspot wrasses usually established their territories along reef edges where spawning occurred. Furthermore, site B encompassed half of a patch reef (Fig. 1). Because the tailspot wrasse usually resided and moved in the reef flat of the fringing and patch reefs, we made topographical maps of the reef flat of both sites before performing behavioral observations. We did this by surveying the entire area of each site with a 2×2 m grid quadrat and recording potential fish shelters (such as hard corals, soft corals, coral rubble, and crevices) more than 15 cm in diameter. Because the tailspot wrasse is a small labrid fish (<12 cm in total length;

see Kuwamura et al. 2000), these corals and rubble were large enough for shelters of the wrasse. From the maps, we calculated the area of reef flat in which fish could potentially move freely, as well as the total area of the shelters in both sites using a digitizer (Wacom ArtPad II pro).

We observed fish behavior during the reproductive season from the end of April until early October in 1995 (site A) and in 1996 (site B). To identify individual fish, we collected all fish that spawned within the study sites, using barrier and hand nets, every 1–2 months and tagged each with a small piece of colored plastic as well as measuring body size (total length) to the nearest 0.1 mm. We later marked individual fish with subcutaneous injections of colored dye (alcian blue) or fluorescent elastomer (Northwest Marine Technology) so that we could discriminate individuals who had lost plastic tags. All fish were released at the collection sites after marking.

Because spawning occurred just before sunset, we tracked each TP male from about 1 h before sunset until the fish burrowed itself into the sand to sleep (Kuwamura et al. 2000). We observed one to four males on each evening, except on days with bad weather conditions (i.e., typhoons). During each daily observation period, we recorded the number of females who spawned with the male and the identity of each. We also recorded each male's patrolling area in which the owner chased away other intruding males, and referred to this area as the male's territory. Males usually moved intensively within their territories and courted females at dusk. However, in the presence of predators such as lizardfishes (Synodontidae), males typically stopped near shelters and showed a particular display, bobbing their heads up and down. This head-bobbing display was performed only when they were faced with predators, so it seems that the display is one of the "pursuit deterrence displays" (Smith 1997). Because most predators such as lizardfish assumed cryptic coloration and behavior, it was difficult to accurately count the number of predators within the study sites. Indeed, observers often noticed predators only after the occurrence of male head-bobbing displays. Therefore, we counted the number of head-bobbing displays against predators and used it as an estimate of predation pressure during the observation period. We also counted the number of attacks by predators toward male tailspot wrasses as well as toward females spawning with or being courted by these focal males.

To determine individual female home ranges, we followed each female for 5–10 min or checked their positions during the day (1000–1800) every 1–4 weeks. Before spawning at dusk, females moved from their home ranges to spawning sites within male territories, keeping themselves under cover during the trip. We measured the distance of each such female spawning trip as the linear distance between the center of the female home range to their spawning site. To determine the mating situations in the study population, we categorized females into the four following types on the basis of the relationship of their home range positions to male territories and to their mates. In type I, the female's home range was contained within the territory of a male who mated her; type II, the female's home range was
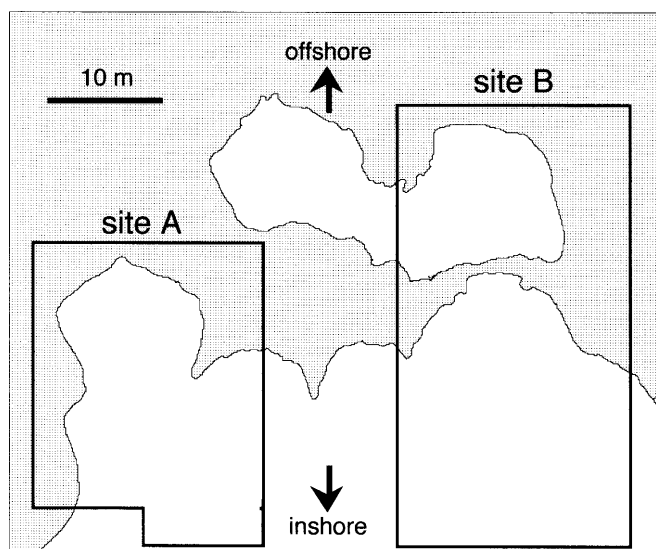
Fig. 1. Study sites A and B. *Open areas*, reef flat in which fish resided and moved; *shaded area*, sandy bottom over reef edge

partially overlapped with her mate's territory but also overlapped with those of other males; type III, the female's home range was contained within a male territory but she mated with another male; and type IV, the female's home range did not overlap with any male territories and she moved to a given male territory to spawn.

We analyzed the opportunity for female mate choice by focusing on the female mate-change behavior. Females appeared to change mates (spawn subsequently with a different male) in two social contexts. The first such situation was when there were spatiosocial changes in the environment, such as shifts in male territories and disappearance of previous mates because of mortality or male–male competition. In the second context, mate changes occurred without any of these changes in spatial environment, such that the mate changes may be based upon an actual choice. Therefore, we counted the number of mate changes for each female spawning more than once during the observation period (i.e., those which had a chance to change their mates), and categorized the mate changes as occurring in either of the foregoing social contexts.

Results

Site A had a smaller reef flat area ($347.1\,m^2$) than that of site B ($531.1\,m^2$), but the total area of shelters of site A ($170.3\,m^2$, 49.0% of the reef flat area) was greater than that of site B ($103.6\,m^2$, 19.5%; Fig. 2).

During the observation period, a total of 6 and 9 TP males appeared in site A and B, respectively. However, at any one time during the study, there were 3–5 males with established territories at both sites. When a male had disappeared, in general, the neighboring male or a new male that came from the outside of the study sites shifted and reoccupied the vacant territory. Males at site B disappeared more frequently, perhaps the result of predation because they were never found around the study area. However, the number of "missing" and "remaining" males (3 in both sites) in late August did not differ significantly (Fisher's exact probability test; $P > 0.6$). The number of females who spawned more than once during the observation period was 34 and 28 for site A and B, respectively. These marked females seldom shifted the location of their home ranges and never emigrated into another study site during the observation. In late August, 17 and 11 of these remained within site A and B, and the numbers of remaining and missing females did not differ between the two sites (Fisher's exact probability test; $P > 0.4$). The proportion of the numbers of males and females did not differ significantly between the two sites (Fisher's exact probability test; $P > 0.3$).

The number of spawnings observed was greater in site A than that in B (Table 1), reflecting the difference in total observation time (232 h in sites A and 79 h in B, respectively), depending on the manpower of each year. In more than half the spawning events at both sites, females mated with males whose territories encompassed their home ranges (type I; Table 1). This tendency was stronger in site

Fig. 2. Distribution of terminal phase (TP) male territories (*thick solid lines*) and female home ranges (*thin solid lines*) within sites A (June 12–24, 1995) and B (August 15–19, 1996), respectively. *Broken line*, reef edges; *shaded areas*, potential fish shelters (only those >0.5 m in length are shown) such as corals, rubble, and crevices
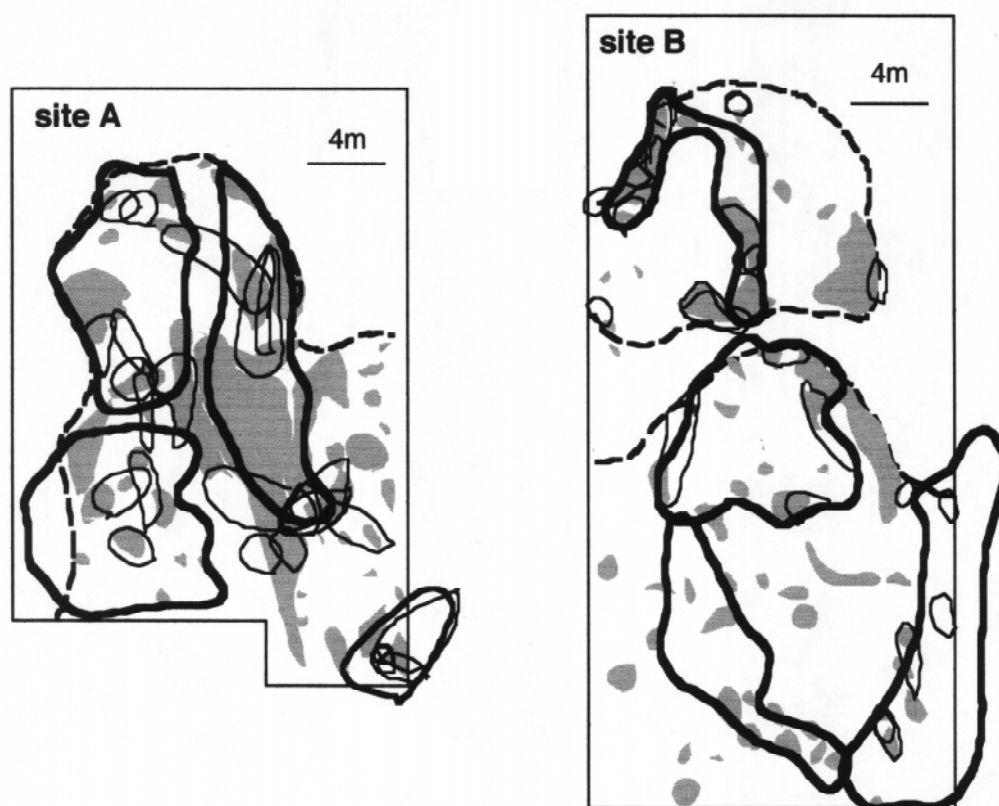
Table 1. The number of spawnings by females that spawned more than once during the observation period

	Site A	Site B
Total no. of spawnings	544	186
No. of spawnings by females whose home ranges were:		
Type I: contained by their mates territories	301 (55.3)	137 (73.7)
Type II: partially overlapped by their mates territories	70 (12.9)	19 (10.2)
Type III: located within territories of males other than their mates	109 (20.0)	9 (4.8)
Type IV: not overlapped with any male territories	64 (11.8)	21 (11.3)

Spawning events were categorized into four types by location of the females' home ranges and that of male territories
Numerals in parentheses show percent of the total number of spawnings

Table 2. Frequency of female mate changes in sites A and B

	Site A	Site B
a. Number of females that changed mates:		
Total no. of females that spawned more than once	34	28
No. of females that changed their mates at least once	30 (88.2%)	13 (46.4%)
No. of females that changed mates without apparent change in spatiosocial environment (female mate choice alone)	29 (85.3%)	3 (10.7%)
b. Number of spawnings and mate changes for each female:		
Median (range) of no. of spawnings	11 (2–44)	6 (2–14)
Median (range) of no. of mate changes by mate choice alone	3 (0–22)	0 (0–3)

B, however, and the females of site A spawned more frequently with other males whose territories did not overlap with female home ranges (type I + II versus type III + IV; Fisher's exact probability test, $P < 0.001$; Table 1).

More females at site A changed mates than those at B (Table 2). For most females at site B (10 of 13), comparing with females at site A (1 of 30; Table 2a), mate changes were seen only in the context of spatiosocial changes (mate disappearance or shifts in male territories). In the context of no apparent spatiosocial changes and, thus, based on their actual choice, more females changed mates at site A than site B (29/5 versus 3/25; Fisher's exact probability test, $P < 0.001$; Table 2a). In addition, in the same social context, individual females changed mates more frequently at site A than at site B (Table 2b). These site A females changed their mates in nearly a quarter of spawning events (median, 23.2%; range, 0%–81.5%) with almost no mate change for site B females (median, 0%; range, 0%–60.0%; Mann–Whitney U-test, $z = -5.3$, $P < 0.001$). The mate-change rate by each female's actual choice did not correlate significantly with their body sizes in both sites (Spearman's rank correlation coefficient: $r_s = -0.11$, $P > 0.6$, $n = 22$, site A in June; $r_s = -0.01$, $P > 0.7$, $n = 26$, site B in June). Females at site A performed longer spawning trips from their home ranges to territories of their mates (median of mean for each female, 7.3m; range, 1.1–25.8m) than females at site B (median, 5.0m; range, 0.5–12.0m; Mann–Whitney U-test, $z = -2.3$, $P < 0.05$).

Males frequently performed head-bobbing displays against predators (Table 3), especially toward lizardfishes such as *Synodus dermatogenys* and *Saurida gracilis* (98.3% and 95.7% for sites A and B, respectively) and occasionally toward the cornetfish *Fistularia commersonii*, the trumpetfish *Aulostomus chinensis*, and groupers, *Epinephelus* spp. Males or females near courting and spawning males were sometimes attacked by these predators (Table 3). In one case at each site, the predator succeeded in catching a tailspot wrasse. Fish at site B were attacked by predators more often than those in site A (Fisher's exact probability test; $P < 0.001$), although males at site B faced and displayed against predators only about one-third as much as those of site A per unit time (Table 3).

Discussion

Colin and Bell (1991) briefly reported the mating system of the tailspot wrasse as harem polygyny. However, the present study revealed the tailspot wrasse in the study population showed a male-territory-visiting polygamy (for terminology, see Kuwamura 1996, 1997) rather than the harem polygyny. Females often moved and mated with males whose territories did not contain or overlap with their home ranges, or some female home ranges did not overlap with any male territories. Furthermore, females, especially

Table 3. Frequency of male head-bobbing displays against predators and attacks from predators toward males or females near courting and spawning males

	Site A	Site B
No. of male displays against predators (per 100 observation hours)	814 (351.6)	92 (116.0)
No. of attacks from predators toward males or females (per 100 observation hours)	9 (3.9)	7 (8.8)

at site A, often changed mates under the context of no apparent change in spatiosocial environment.

These mate changes without any changes in spatiosocial environment appear to be the result of female mate choice alone. Because female tailspot wrasses have clear mate choice criteria such as brighter body coloration and larger body size of males (Kuwamura et al. 2000), females are likely to change their mates if preferable males are available. The mate changes by female mate choice may also occur when the coloration of the previous males becomes duller at the next mating, because male coloration frequently changed depending on their condition (our unpublished data), similar to other fishes with sexual dichromatism (Dugatkin and FitzGerald 1997).

Compared with females at site A, females of site B changed mates much less frequently, and mated more often with the nearest males whose territories contained their home ranges. This difference did not result from the shortage of potential mates, because more males established territories at site B throughout the observation period. Moreover, females at site A often changed mates from nearby males to more distant males and thus conducted longer spawning trips to male territories. These results suggest that the lower frequency of female mate changes in site B might have been caused by higher predation risk during spawning trips. Fish in site B were more frequently attacked by predators, although the density of predators, estimated by the frequency of male head-bobbing displays against predators, was only one-third of that in site A. Under high predation pressure, as in site B, females should not conduct longer spawning trips to reduce the risk of predation. Such trade-off between mate choice and costs of longer spawning trips has been reported from other reef fishes (Reynolds and Côte 1995; Karino and Kuwamura 1997; Sikkel 1998). The costs of spawning trips of those fishes, however, did not include predation, but intra- and interspecific attacks or loss of food (algae) in their territories. Thus, female tailspot wrasses might change their behavior more dramatically according to the predation risk than females of those fishes.

The difference of predation risk between the two sites may have resulted from the difference in topography of microhabitats. Because the reef flat of site A was much more covered by shelters such as corals and rubble than that of site B, females could conduct longer spawning trips safely by hiding themselves under those objects. Therefore, females at site A could change their mates frequently according to true mate choice. In contrast, females at site B did not

have sufficient shelters for safe spawning trips to change their mates, and so should have mated with the nearest males in most cases. In the cricket *Gryllus integer*, females also became less choosy under low coverage and, thus, high predation risk (Hedrick and Dill 1993). Under high predation risk, the pipefish *Syngnathus typhle* began to copulate with mates after a small amount of courtship, suggesting they traded information concerning mate choice such as mate quality for a reduction in predation risk (Fuller and Berglund 1996). In the tailspot wrasse, females at site B may also trade mate assessment during long spawning trips for reducing predation risk.

Houde and Endler (1990) and Endler and Houde (1995) have revealed that female preference of guppies for conspicuous male coloration was negatively associated with predation risk in each population. The female choosiness of guppies was determined on a genetic basis: laboratory-reared females descended from populations under high predation risk showed less choosiness even they had never seen predators (Houde and Endler 1990; Endler and Houde 1995). Because the eggs and larvae of the tailspot wrasse are pelagic (Colin and Bell 1991; Kuwamura et al. 2000), juveniles would not always settle on or recruit to their native reefs. Thus, the difference in female choosiness between the two sites was not determined genetically but by plasticity of female reproductive tactics according to the predation risk in each microhabitat where they had settled.

The results of this study strongly suggest that the predation risk influenced on female mate-change behavior and the distance of spawning trips. However, this study compared field data from the different sites in different years, and so it is possible that other factors also caused the difference of the behavior of these females. For example, when the water turbidity and thus visibility differ between the two sites or years, it can be expected that females would incur a greater cost for mate-searching behavior and would reduce their choosiness under situations of low visibility, although we detected no apparent difference in water visibility between the two years. Further examinations, such as predator removal experiments, are needed to clarify the degree of effectiveness of predation risk on the opportunity of mate choice in female tailspot wrasses.

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